AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3553, 11 pp., 9 figures, 1 table March 8, 2007

A Lateral Gynandromorph in the Bee Genus *Thyreus* and the Sting Mechanism in the Melectini (Hymenoptera: Apidae)

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ABSTRACT

A lateral gynandromorph of *Thyreus redactulus*? Cockerell is described and figured, with a particular emphasis on the genitalic sclerites. As such, the sting morphology and mechanism are described for *T. ramosus* (Lepeletier de Saint Fargeau) to provide a comparative framework for understanding the gynandromorph. The implications of the gynandromorph's genitalic arrangements for intersexual homologies are explored.

INTRODUCTION

Sex anomalies occur relatively frequently among bees and may be of striking appearance in species where the two sexes are markedly dissimilar in structure or color. Although sex anomalies appear to be more common among the Megachilidae[2], this is likely a result of the particular fascination with the recognition and documentation of such anomalies by the late Theodore B. Mitchell, a specialist on this family (e.g., Mitchell, 1929). More recently, Wcislo et al. (2004) have partially summarized the variety of documented sex anomalies (omitting intersexes), and gynandromorphs have been implicated in the development of male-like traits in cleptoparasitic females (Cockerell, 1911; Wcislo, 1999).

Most papers, particularly among the more recent literature, have confined themselves to consideration of the external characters, perhaps owing to concern not to risk damage to valuable specimens. However, as many docu-

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[2] Highlighting this fact, normal females of the former subgenus *Androgynella* (a synonym of *Eutricharaea*), when originally proposed (originally as a separate genus before being placed in *Megachile*), were unknown—hence, its name.

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mented sex anomalies have been, apparently, intersexes, the absence of information on possible modifications of the genitalia is perhaps not serious. True gynandromorphs are, as Mitchell (1929) and Wcislo et al. (2004) document, of relatively rare occurrence among the bees, but a number have been more or less fully recorded.

Lateral gynandromorphs, where the sagittal division of the insect into male and female halves may extend to the genitalia, are of particular interest as a potential source of information on homologies between the structures contributing to the male and female genitalia. From the Anthophila, examples have been described and figured by Bischoff and Ulrich (1929: for *Chalicodoma*) and by Popov (1937: for *Halictus*). The present paper deals with a lateral gynandromoph of an Indian species of *Thyreus* (Melectini), and, since the study of this specimen necessitated investigation of the structure and mechanics of the sting in normal female *Thyreus*, with the latter subject also. In general, the genitalic morphology in Melectini has not been investigated outside of the usual taxonomic description of the male terminalia. Among melectines, the sting morphology has been adequately described only for a single species of *Thyreomelecta* (Rightmyer and Engel, 2003).

TERMINOLOGY

It may be recapitulated that in the Apoidea, like all Apocrita, the first abdominal segment forms part of the mesosoma. For this reason, I have numbered the segments throughout this paper based on their metasomal rather than abdominal count. In other words, the "sixth sternum" referred to herein is that of the metasoma, or the seventh *abdominal* sternum (= sixth *metasomal* sternum). In *males* there are therefore nine metasomal segments (abdominal segments 2–10). Seven terga are usually exposed, tergum VIII being invaginated, weakly sclerotized, and closely applied to the inner surface of tergum VII. A lesser number of sterna are usually exposed, sterna VII and VIII being invaginated (in the Megachilidae, where tergum VI commonly forms the apparent apex of the metasoma, its apical area and the little-exposed tergum VII forming part of the ventral surface of the metasoma, the number of exposed sterna may be greatly reduced). In *females*, six terga are usually exposed, terga VII (which retains its spiracular openings) and VIII being always invaginated and dissociated into hemitergites that are closely associated with the sting mechanism proper. Ventrally, six sterna are usually exposed, the sixth frequently modified to accommodate exsertion of the sting.

Among genitalic structures proper I have generally followed the terminology of earlier authors, although I have employed the term furcula (as used by many authors: e.g., Packer, 2003; Rightmyer, 2004) for the dorsal, wishbone-shaped, or merrythought-shaped structure arising from the convergence and fusion of the structures referred to by Michener (1944) as the apodemes of the stylet. The structure usually termed the gonostylus and also variously known, in the Hymenoptera, as the third valvula, ovipositor sheath, sting palpus, or dorsal or lateral valve (or accessory lobe) of the second valvifer, is homologous neither with the styli (distal processes of the coxopodites) of the Zygentoma and some Pterygota nor with the first and second valvulae (Snodgrass, 1935). Neither of the terms gonostylus nor third valvula, therefore, is morphologically correct. Recognizing the possible confusion in terms of homology across broader groups, Scudder (1961, 1971) proposed the term *gonoplac*[3] for this structure. For the Apoidea, however, where the structure in question is most often styliform and where no other structure is referred to as a stylus, the term gonostylus has continued in use and, if employed in strictly a descriptive sense, poses no confusion. Similarly, the first valvifer of Hymenoptera has been lost and is replaced by the *gonangulum*[4], a basal differentiation of the second valvifer that articulates with the ninth abdominal tergum (eighth metasomal tergum

[3]It should be noted that the term "gonoplac" is perhaps malformed in Greek. It is presumably derived from γονή + πλαξ. If so, its forms in third declension πλακος and gives in Latin third declension *plax, placis* (i.e., gonoplax).

[4]It should be noted that the term "gonangulum" is a hybrid of Greek and Latin. Perhaps a more linguistically favorable term would be *gonogonium* (Greek) or, perhaps, something like *semiangulum* (Latin).

in Apocrita), the second valvifer, and the first valvulae in Dicondylia (Scudder, 1961, 1964; Grimaldi and Engel, 2005). Despite this, many melittologists persist in referring to this structure as the first valvifer (or gonocoxa) or "triangular plate". Terminologies should ideally, of course, be valid both morphologically and descriptively. In practice this is rarely achieved, owing, on the one hand to changing morphological concepts and, on the other, to the difficulty of finding terms that are both sufficiently elastic to accommodate all the forms in which a given morphological unit may be expressed and sufficiently distinctive to obviate confusion with all other terms in use. It seems probably that descriptive terminologies will long be required to supplement morphological terminologies. Nonetheless, herein I depart from melittological tradition and employ the terms gonoplac and gonangulum.

As some of the structures referred to in this paper lie in an inverted and reversed position when the sting is retracted, it is necessary to note that such terms as dorsal and basal and their opposites are used, unqualified, in a morphological sense.

DESCRIPTIONS

Thyreus Sting Morphology

Thyreus ramosus (Lepeletier de Saint Fargeau)
figures 1–3, 9

Comments: Tergites VII and VIII are dissociated into lateral, sclerotized hemitergites, their medial, dorsal areas becoming membranous and elastic to accommodate the movements of the sting and associated structures during exsertion. Although completely invaginated within the genito-anal atrium, the seventh hemitergite retains its spiracular openings; in the eighth hemitergites, they are lost. The hemiterigites of the seventh metasomal (last spiracular) segment are small and weakly sclerotic. They occupy a lateral position between the lateral processes of the sixth sternum (with which they are loosely articulated, this articulation forming the pivot on which the sting mechanism rotates when the sting is exserted) and the basal extremities of the apodemes of the hemitergites of the eighth segment, with both of which they are loosely connected (cf. figs. 1, 2). The hemitergites of the eighth segment are relatively large, weakly sclerotic, and broadly united with their equally large, scaphoid apodemes. Dorsally, each hemitergite becomes membranous and is applied to the outer surface of the apical half of the second valvifer; postero-ventrally, it articulates with the small, strongly sclerotic gonangulum. The second valvifer consists of a rigid, well sclerotized anterior costa, which articulates laterally with an angular projection of the gonangulum and is prolonged dorso-apically in the distinct, terminally hamate costal process (where the proctiger connects) and a broad, membranous limb from which arises, dorso-apically, adjacent to the costal process, the gonoplac. The gonoplac consists of a simple basal article (or *stylifer*) and a distinct, more strongly sclerotized, setigerous apical article (or *orthostylus*). The gonangulum and second valvifers give rise ventrally to the first and second valvulae. The rami of the valvulae are slender, elongate, and in contact throughout their length—that of the second valvula supports the ventral margin of the limb of the second valvifer. The sting (comprising the lancets of the first valvulae and the stylet of the dorsally fused second valvulae) is long and heavy and occupies the whole length of the sixth sternum. The furcula is broad, subcordate, and apically appendiculate, and its two arms are closely but freely articulated at the sides of the bulb of the stylet basally (cf. fig. 9).

Thyreus Sting Mechanism

The sting and its associated structures in *Thyreus* (including, in a wider sense, the sixth sternum, the hemitergites of the seventh and eighth segments, and the gonangula and second valvifers) are typical of those of the parasitic Apinae. The sting is enlarged, and the metasoma has correspondingly undergone modification in two complementary directions to house the retracted sting (which may extend basad beyond the apical margin of the second sternum; cf. fig. 1) and to accommodate the extended range of movements necessary for its full exsertion.

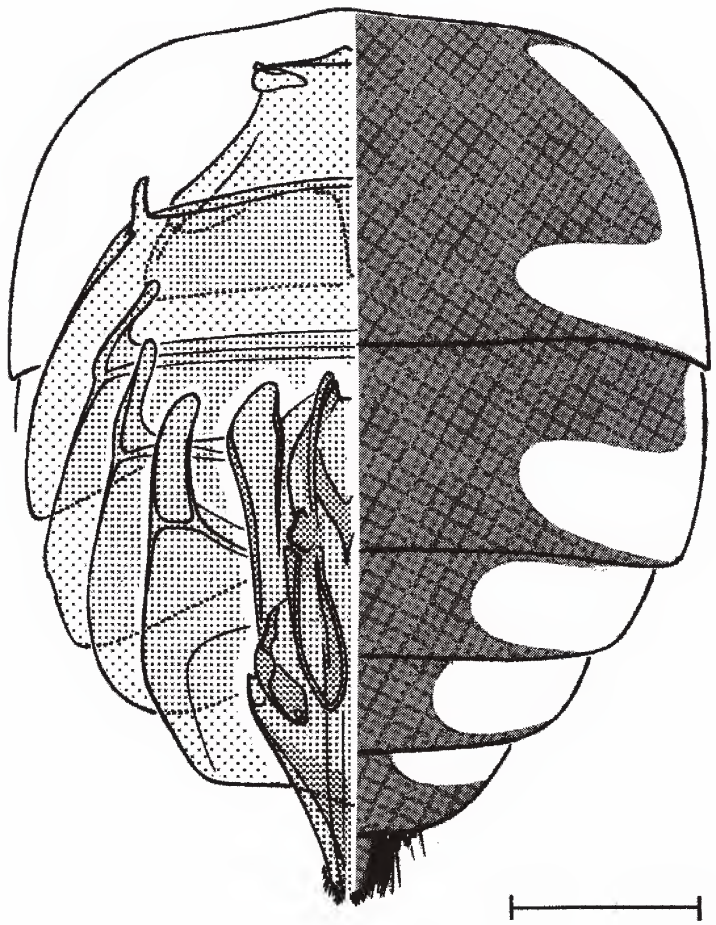


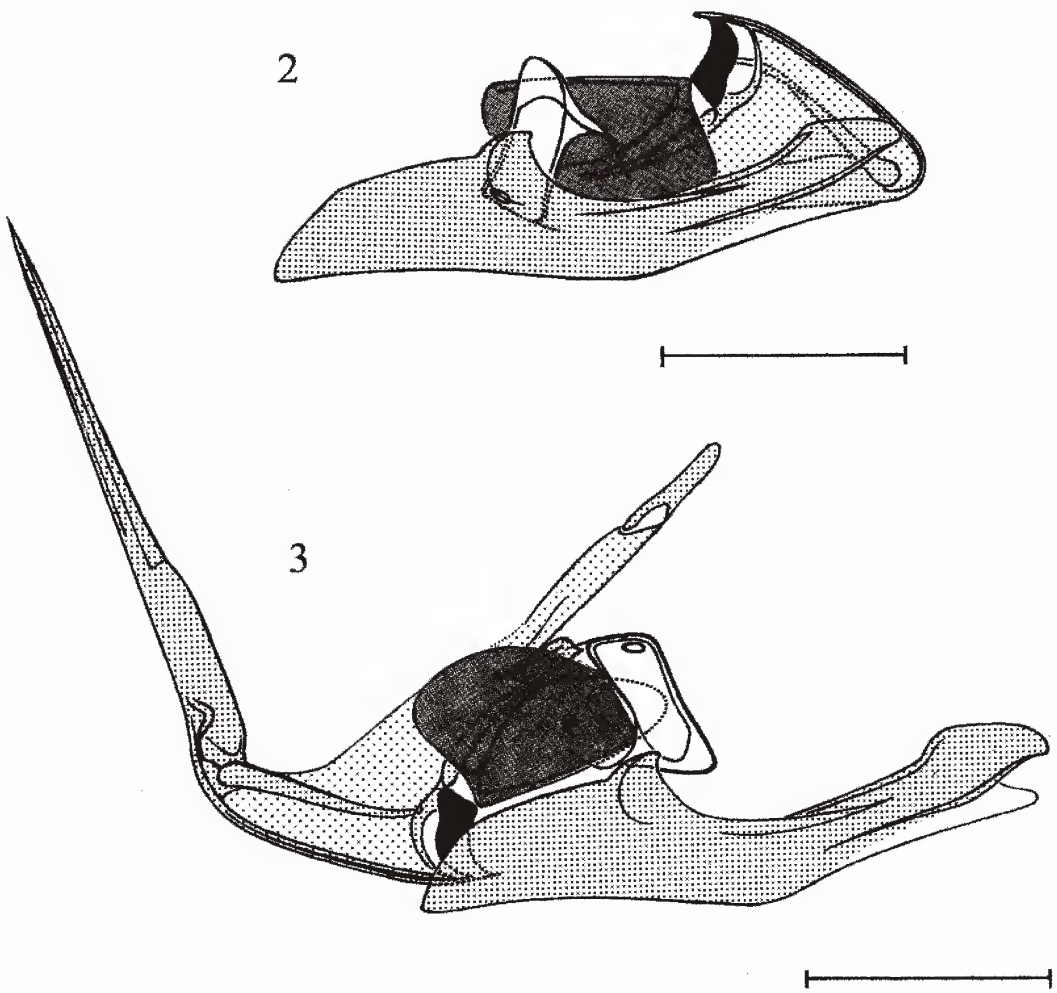
Fig. 1. *Thyreus ramosus* (Lepeletier de Saint Fargeau), dorsal view of female metasoma depicting genitalia in situ. Scale bar = 1 mm.

The sixth sternum, which forms the floor of the sting atrium, is large, elongate, and trough-shaped. Postmedially, it carries a pair of angular lateral processes that are indirectly connected (through loose intermediate connections with the hemitergites of the seventh segment ventrally) with the apodemes of the hemitergites of the eighth segment basally to provide an axis about which the sting and its more intimately associated structures (the hemitergites of the eighth segment and the gonangula and second valvifers) may rotate on exsertion or retraction. Apically it is narrowed, and its sides are more strongly reflexed and incurved to form a semi-tubular sting guide.

The other structures associated with the sting have already been described (*vide supra*).

The Retracted Sting

When the sting is retracted (fig. 2), the hemitergites of the seventh metasomal segment are inverted, and the hemitergites of the eighth segment, with the gonangula and second valvifers, are inverted and displaced basad, as the result of rotation (in an anticlockwise sense as seen from the right side) about the lateral processes of the sixth sternum. The costal processes of the second valvifers and the gonostyli are accordingly displaced ventrad and directed apicad and are located with the stylet in the trough of the sixth sternum. The rami of the first and second valvulae are located dorsally and directed basad and ventrad to a point above the membranous anterior margin of the sixth



Figs. 2, 3. *Thyreus ramosus* (Lepeletier de Saint Fargeau), female, lateral view of genitalia, setae omitted; seventh hemitergite not shaded or stippled; eighth hemitergite densely shaded; gonangulum solid black; second valvifer stippled; furcula, sting, and sixth sternum (except anterior weakly sclerotized area) densely stippled. **2.** Position of sclerites with sting retracted. **3.** Position of sclerites with sting exserted (the sting is shown drawn away from the sting guide to make the relative positions of the furcula and the rami of the valvulae clearer). Scale bars = 1 mm.

sternum (between the basal extremities of its apodemes), where they are abruptly flexed apicad immediately before the origin of the sting. The furcula is directed dorsad and apicad, with its appendix located in the conjunctiva between the bases of the valvifers and gonangula.

The Exserted Sting

When the sting is exserted (fig. 3), by means of forces generated in the anterior part of the metasoma, the hemitergites of the seventh and eighth segments rotate clockwise around the lateral processes of the sixth sternum—the former through about 140°, when their spiracles regain a normal, dorsal position; the latter through about 160°, bringing their points of articulation with the gonangula into a ventral position near the base of the sting guide. The gonangula and second valvifers are now erect (with the costal processes of the latter and the gonostyli separated from the sting and directed dorsad and basad), the rami of the first

and second valvulae are directed apicad and located in the sting guide, and the base of the sting lies near the apex of the guide. Concurrently with the rotation of the hemitergites, the furcula hinges clockwise on its articulations with the base of the sting and, as the sting travels back through the sting guide, describes an angle of about 150°, coming to rest in a plane a little above that of the rami of the valvulae, where it functions as a strut between the base of the sting (above the insertion of the rami of the valvulae) and the region of the inter-valvifer articulations. These movements may be readily demonstrated in preparations from dried material.

Simultaneously with these movements within the sting atrium, the sixth sternum (which externally is largely enveloped by the latero-ventral lobes of the sixth tergum) is itself partially exserted. This movement, and the upward probing or stinging movements of the apical segments of the metasoma repeatedly observed in living material, are presumably enabled by the great development of the sternal apodemes (cf. fig. 1). While in dried material the sting, when exserted, is not usually exposed beyond about the middle of the bulb (and then issues from the apex of the sting guide), in a few instances it may be found fully exserted and directed upward through the dorsal commissure of the guide. The gonoplacs are not exserted but remain within the sting atrium: having no capacity for movement independent of that of the second valvifers, they become (as mentioned) separated from the sting with the rotation of the gonangula and valvifers. Although the apices may just protrude from the opening of the sting guide when the sting is retracted or only slightly exserted, and consequently the apices may be presumed to retain a limited sensory function, it is apparent that their usefulness as "sting palpi", to revert to an older term, has become sensibly diminished.

Thyreus Gynandromorph

Thyreus redactulus? Cockerell
figures 4–8

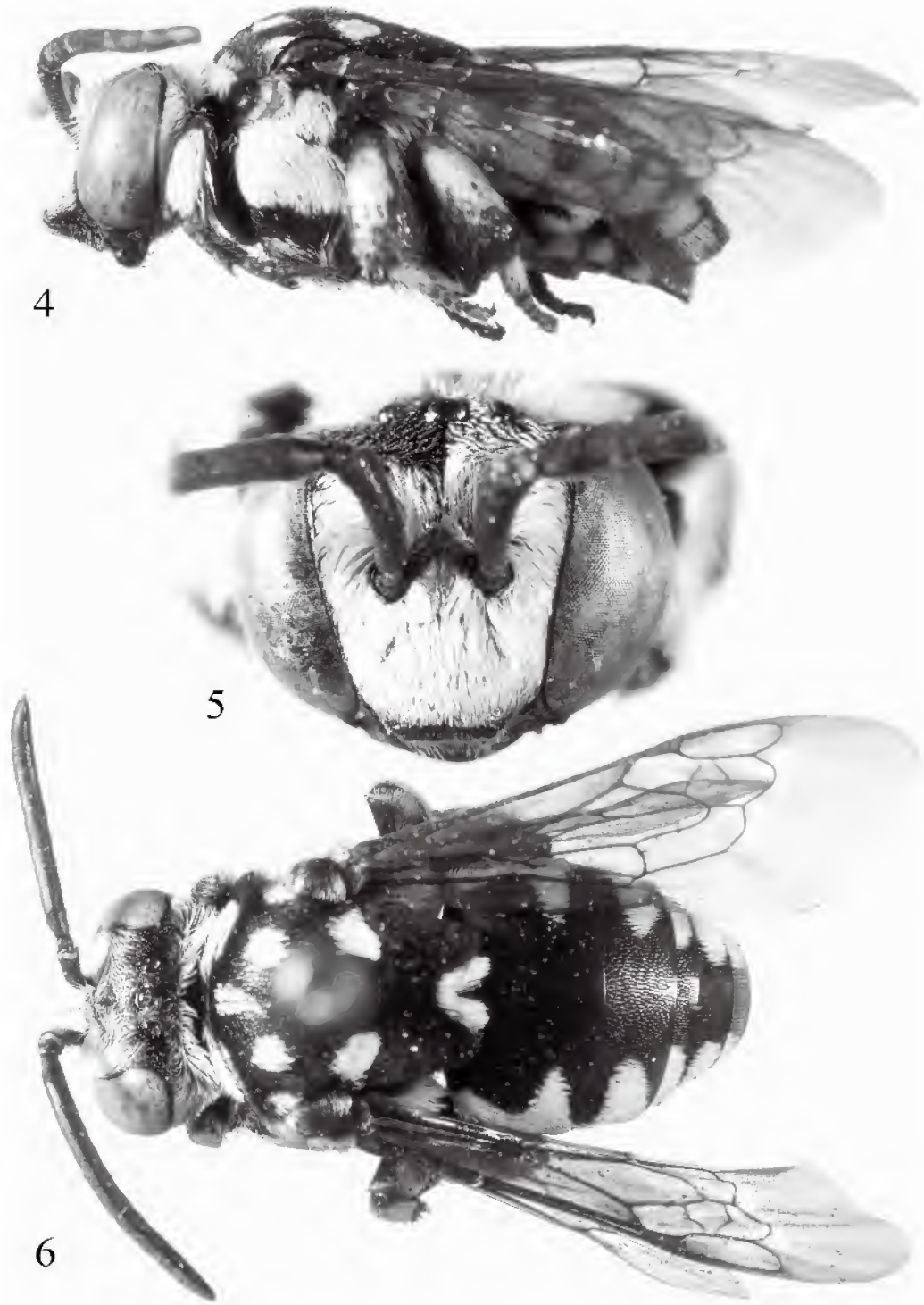
Material: South India, Coimbatore, 30.iii. 1950, P. S. Nathan. Genitalia dissected and permanently set in slide mount associated with the specimen. Deposited in the Division of Entomology, University of Kansas Natural History Museum. The specimen is almost assuredly an individual of *T. redactulus*. Nonetheless, I have been slightly hesitant with the identification, as noted by the interogative mark after the epithet, given the distortion of genitalic structures.

Comments: The gynandromorph is on the left side, male; on the right side, female. The left antenna is that of the normal male (i.e., with 13 antennal articles), the right that of the normal female (i.e., with 12 antennal articles). Structural differences between the two sides of the head, mesosoma, and first through fifth metasomal segments are otherwise unremarkable (e.g., figs. 4–6). The legs show a mixture of male and female characters, and on the male side the modifications of the metafemora and metatibiae characteristic of species of the *takaonis* group are not developed. The condition of the apical segments of the metasoma and of the genitalia is more complex.

The metasoma is modified by the apparent loss of the eighth segment on the male side and on the female side by a retrogressive, intersegmental transfer of characters that results in the appearance of a supernumerary exposed segment and in a corresponding decrease in the number of concealed terga, which reduce to one. The principal effect of these modifications is the bringing together in one segment (the seventh) of the male and female halves of the genitalia, the genitalia of the normal male being located between the eighth tergum and the eighth sternum, invaginated within the seventh segment, and those of the female within the sixth segment between the hemitergites of the seventh and eighth segments (which are displaced laterad and modified to form part of the sting mechanism). There are, therefore, seven exposed terga and six exposed sterna.

The sixth segment has the appearance of a normal intermediate metasomal segment. On the right, the special characters of the normal female sixth tergum, in particular the pygidial process, are entirely suppressed.

The tergum of the seventh segment is irregularly developed and, particularly laterally, only weakly sclerotized. The left half tends to the form shown in a normal male, the



Figs. 4–6. *Thyreus redactulus*? Cockerell, gynandromorph. **4**. Lateral aspect. **5**. Facial aspect. **6**. Dorsal aspect.

right half to that shown by the preceding tergum in a normal female, the normal condition, that of a small, wholly invaginated and laterally located hemitergite, being entirely lost. The tergum is fimbriate apically, but a pygidial plate is not developed. The apparent sternum of the same segment is a broad, weakly sclerotized plate, closely adapted on the left to the anteroventral surface of the gonobase and on the right underlying the female genitalia basally. On the female side, neither this sternum (which, with that of the eighth segment, is not present as a separate sclerite in the normal female) nor that of the preceding (sixth) segment shows any tendency toward the highly distinctive form of the sixth sternum in a normal female.

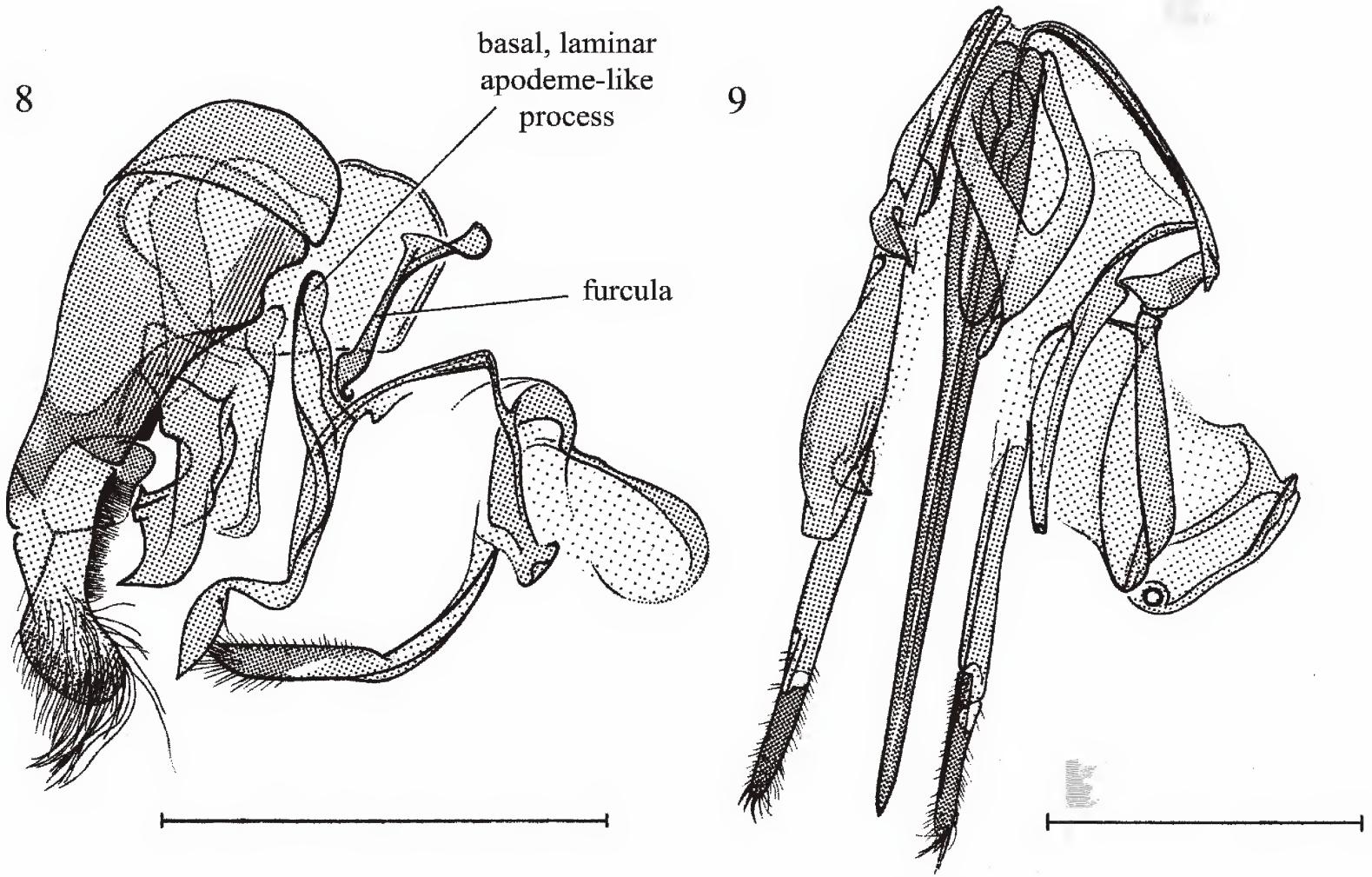
The eighth segment, on the male side, is either entirely lost or, at least, not represented by a separate sclerite; on the female side, the hemitergite approaches the normal form, particularly in the apodeme, but is only weakly sclerotized.

The genitalia (figs. 7–8) are, on the left side, substantially normal male; on the right, abnormal female with male tendencies. The hemitergite of the eighth segment, the second valvifer, the gonoplac, and the rami of the valvulae are relatively little altered and immediately recognizable, the most noticeable modifications lying in the contraction and strengthening of the costal process of the second valvifer and in the expansion of the gonoplac. The second valvula forms an imperfect and twice geniculate stylet ending in a distinct, pointed bulb, which does not, however, represent the bulb of a normal sting but a contraction of the apical part of the stylet. The bulb bears a single, strong seta. The strong, erect, laminar basal process (fig. 8), suggestive of the highly developed sternal apodemes found in *Thyreus* (cf. fig. 1), does apparently represent the right side of the bulb of a normal sting. The equally strongly sclerotized structure (fig. 8), articulated at the base of the sting laterally, is clearly the right half of the furcula. Its presence in addition to the apodeme-like process of the sting, and its free articulation with the base of the bulb, render suspect earlier identifications of the furcula as the "apodeme of the stylet" (and, accordingly, such terminology).

Fig. 7. Photomicrograph of dissected genitalia of *Thyreus redactulus*? Cockerell gynandromorph.

DISCUSSION

A study of the terminalic sclerites and their articulations in the present gynandromorph (fig. 8: a normal female in similar orientation is depicted in fig. 9) suggests the intersexual homologies outlined in table 1. The principal homologies indicated stand in full agreement with those suggested by the gynandromorphs of *Chalicodoma* and *Halictus* recorded by Bischoff and Ulrich (1929) and by Popov (1937), and with the conclusions arrived at by Michener (1944) following a general review of the question of homologies between the male and female genitalia in bees. Some potential refinements of the previously established homologies are, however, supported by the development and articulation of sclerites in the present gynandromorph. In particular, that the apodemes of the penis valve correspond with a basal prolongation of the side of the bulb of the stylet, and not with either a development of the ramus of the second valvula or an arm of the furcula ("apodeme of the stylet"), is abundantly clear from the manner of entry of the ramus and the joint presence of both the apodeme-like structure (fig. 8) and the entirely separate half-furcula (fig. 8). Similarly, it is tempting to see in the furcula, as a common dorsal structure lying above and closely associated with the bulb of



Figs. 8, 9. Genitalia of *Thyreus* species. **8**. *Thyreus redactulus*? Cockerell, gynandromorph, dorsal view. **9**. *Thyreus ramosus* (Lepeletier de Saint Fargeau), female, genitalia and right seventh hemitergite, oblique dorsal view (lateral halves of genitalia slightly separated). Scale bars = 1 mm.

TABLE 1
Intersexual Homologies Suggested by Present Gynandromorph

Male	Female
Gonobase Gonocoxa	Second valvifer[a]
inner apical process of gonocoxa	costal process of second valvifer?
Gonoplac (="Gonostylus")	Gonoplac[b]
Penis valve	Second valvula
apodeme of penis valve	bulb of stylet (in part)
bridge of penis valve	furcula?

[a]The gonobase is developmentally a basal, secondary division of the gonocoxae; thus, the gonobase and gonocoxae are together homologs of the second valvifer.

[b]The female gonoplac clearly shows an intermediate condition, including a shift of sclerotization toward the apices of the orthostylus.

the stylet, the homolog of the bridge of the penis valves (table 1), a structure that is well developed in many bee lineages, including the Melectini, and that occupies a similar position.

While the genitalia of the present gynandromorph thus provide direct confirmation of established homologies, the conditions shown by the apical segments of the metasoma are likewise of some interest. Certainly, the appendicular origin of male genitalic sclerites in certain pterygotes, particularly some Holometabola, is of some debate. As has been noted by previous authors, however, if the male and female genitalia of Hymenoptera were of entirely independent origin, the one a phallic structure borne within the eighth metasomal segment (or, more exactly, between the tergum and sternum of the eighth segment invaginated within the seventh segment) and the other a derivative of the coxal or sternal appendages of the seventh and eighth metasomal (eighth and ninth abdominal) somites of the primitive insect (borne in the sixth metasomal segment between the dissociated and laterally displaced hemitergites of the seventh and eighth metasomal segments), the expected condition in lateral gynandromorphs would be that of the independent appearance of the male and female half-genitalia in the segments appropriate to each sex. The condition that is found, on the contrary, is one of the closest associations of these structures in a single, intermediate metasomal segment (i.e., the seventh). The extensive modifications of the apical segments of the metasoma in the present gynandromorph (affecting both halves of the sixth, seventh, and eighth metasomal segments) suggest, in fact, an overriding requirement for the approximation of the male and female half-genitalia, and therefore a strong morphological and ontogenetic connection between them. The present gynandromorph, and others like it, is one more, small element of support for the view that the male and female genitalia of the Hymenoptera are essentially homologous structures (those of the female including certain additional elements). That the female genitalia are of appendicular origin is of little question given the elegant transformation series extending back to the primitive "gonangular" condition seen in Zygentoma (a.k.a., the "lepismatoid" ovipositor) and from there into the even more primitive Archaeognatha. Certainly, male structures across Pterygota are remarkably challenging to homologize, and some have argued that in at least a few lineages these sclerites are of sternal, rather than appendicular, origin and thereby independently evolved and not homologs of female genitalia. If the tight homology between male and female genitalia observed here is correct, then for at least the Hymenoptera the interpretation of a common origin of external genitalic sclerites in both sexes continues to be well grounded (as in Archaeognatha and Zygentoma), as is generally believed by most hymenopterists.

ACKNOWLEDGMENTS

This study initially began as a collaboration with my friend and colleague, the late Dr. Donald B. Baker. Unfortunately, the work had progressed little by the time he passed away in May 2004, although he had prepared illustrations of some structures. Typically, I would have given posthumous authorship to Donald, but as I know we disagreed in some interpretations and conclusions, I do not believe it best to ascribe his name to an article in which the entirety of his ideas is not expressed. Although Donald would have disagreed with me on several points expressed herein, I nonetheless believe it suitable to dedicate this paper to him and his devotion to comparative morphology. I jointly dedicate this work to Dr. Charles D. Michener, who undertook extensive studies of male-female homology, including insights from gynandromorphs, as is done herein, and laid the foundation for the comparative morphology of bees. I am grateful to Dr. Dorothea Brückner and Dr. Antonio Arillo for careful reviews of the manuscript.

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